Foraging decisions in a digestively constrained long-distance migrant, the red knot (Calidris canutus)

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Summary

Animals are continuously making decisions. A lion encountering an impala decides on attacking or neglecting it. A robin in the backyard makes a choice on the number of eggs to produce. Behavioural ecologists aim to understand and possibly to predict the outcome of such decisions. Why does the lion decide to ignore this impala but to attack and slaughter the next one? Why does the robin in one backyard lay four eggs while another one elsewhere lays six? Behavioural ecologists study such decision-making processes from a Darwinian point of view, meaning that they expect animals to choose those options that maximize their number of offspring in the long-term future (fitness). This particular expectation allows behavioural ecologists to make strong predictions. For example, if we assume how fitness scales to the yearly number of consumed impala's, then we can make a prediction on how *often* a lion should attack an impala. Subsequently, through field observations, this prediction can be tested and, in case of falsification, we would adjust our idea about the best possible feeding option (leaving the axiom of fitness-maximisation intact). In this way, theories about animal decision-making arose and are still arising today. For example, the so-called 'optimal foraging theory' covers decisions such as where, what, and when to eat. It is this theory that could bridge a gap to another field in ecology, that of populations and communities. If we can understand and predict how often predators should eat, then we could calculate how *many* predators could be sustained by a given number of prey. In other words, we would then be able to express the population size of the predator as a function of the population size of the prey. Moreover, if we could predict what *type* of prey a predator should select, then we could understand how communities are moulded by the consumer-behaviour of predators. As a next step we could possibly understand how predatory decisions shape the behaviour and life history of prey species in the course of evolution. A killed prey animal is unable to reproduce. Thus, those prey individuals that are not consumed determine what the species will look like in the future (natural selection). For example, if slow impala's are killed

more often than fast impala's and if (at least part of) the variation in speed is genetically-based, then future generations of impala will be able to sprint faster. The other way around, prey mould predators. Those lions that are able to catch the fastest impala's will do better than the slower lions. If variation in speed has a heritable component then future lion generations will be able to sprint faster. Of course, sprinting speed cannot continue to increase forever and is limited by other factors (such as the costs of making and maintaining the sprinting 'machine').

With those abovementioned ideas in mind, we started a project on Texel on this so-called 'evolutionary arms race' between predators and their prey. To keep the study system as simple as possible we chose to work in the relative species-poor soft-sediment communities where only a limited number of invertebrate prey species is consumed by a handful of avian predators. To further simplify matters we selected a mollusc-specialised predator, the red knot (*Calidris canutus*). Molluscs are relatively easily countable and measurable (they do not walk or crawl away fast) and they are able to reproduce under laboratory conditions. Because of that latter habit, we were able to show the heritability of anti-predation traits (dissertation Luttikhuizen). Measurements on the flexibility of their physiology (dissertation Drent) and behaviour (dissertation Edelaar) showed how individual shellfish protect themselves against hungry predators such as red knots. In *this* dissertation we show the other side of the coin: how red knots have evolved into efficient mollusc-eaters and what their limitations are.

Red knots are medium-sized shorebirds (100-200 g) that breed during two months of the year (June-July) in the high-arctic tundra of Greenland, northern Canada, Alaska and Siberia. During the rest of the year they can be found at intertidal mudflats, where they mainly feed on molluscs and to a lesser extent on softer prey species such as crabs or shrimps. Remarkably, they swallow their prey whole, shell and all! The shells are crushed in the gizzard and the crushed shell fragments are subsequently defecated. This is very different to the ways of another well-known shellfish-consumer, the oystercatcher (*Haematopus ostralegus*). This shorebird only ingests the bivalve's flesh by opening the shell with its strong bill. This *in situ* opening of shellfish by oystercatchers is time-consuming and knots seem to have found a faster way to feed on shellfish. However, the knot pays the price for such short external handling times in its digestive tract (moreover, only shells smaller than 2 cm can pass the knot's gape while oystercatchers can feed on all size classes). Red knots crush their hard-shelled prey in their strong muscular gizzards and, when allometrically scaled, gizzards are much larger in knots than in oystercatchers. Large gizzards require large maintenance costs and,

maybe even more important, large transport costs. In other words, knots expend much energy carrying around their heavy gizzards. This is especially the case during their long-distance flights between breeding and wintering grounds (5,000-16,000 km). However, knots seem to have found a solution to this problem. They are able to rapidly reduce the size of their gizzard during the last weeks *before* migratory departure (1-3 wks; 50%-reductions occur regularly). In this way they save a lot of maintenance and transport costs and this mechanism may be a prerequisite to make such long journeys in relatively short time spans. Upon arrival at the wintering or stopover site it takes another few weeks to again increase gizzard size, where after feeding and digestion can proceed at full speed. Knots face an interesting trade-off in these short periods just *before* and *after* their long-distance flights. Namely, it is these periods in which knots should be able to feed faster than during other times of the year. Just *before* the onset of each long-distance flight, knots need to fuel themselves with good amounts of fat to be able to cover the vast distances (usually 80-100 g). Just *after* each long-distance flight they need to replenish their depleted fat stores to normal levels (usually about 20 g). A logical question emerges: how can knots with shrinked gizzards feed that fast? This trade-off between flying with atrophied gizzards while fuelling with hypertrophied gizzards is *the* major theme in this thesis and bears important repercussions on the evolutionary interactions between knots on the one hand and their hard-shelled prey on the other hand.

While studying these 'stomach-problems', we greatly benefited from a methodological breakthrough in ecophysiology. By means of ultrasonography we were able to estimate gizzard mass in live birds. Besides major ethical advantages, this gave us the opportunity (1) to track changes in gizzard mass *within* individuals and (2) to quantify the costs and benefits associated with a given gizzard mass (e.g. rate of digestion (chapter 3), prey choice (chapter 5), patch choice (chapter 6), daily foraging times (chapter 6), and local survival (chapter 11)).

In chapter 2, we used captive knots to experimentally quantify the energetic cost of foraging on hard-shelled prey. We did so by injecting the birds with doubly labelled water, which contains heavy, but stable and therefore safe isotopes of hydrogen and oxygen. These labelled atoms have completely left the body within a few days. The difference between the rate of disappearance of labelled oxygen atoms (^{18}O) and labelled hydrogen atoms (^{2}H) is a measure of carbon dioxide production, which in turn is a measure of the bird's metabolic rate. By offering the food in two ways, either *ad libitum* in a tray or buried in an experimental mudflat, we measured the cost of searching. By offering bivalves with or without shells we measured the cost of shell-crushing. Finally, by

offering either food (without shells) or no food we measured the cost of digestion. It turned out that digesting food was almost twice as expensive as searching for food. In contrast, there was virtually no cost to crushing shells, presumably because the act of crushing happens rather fast.

The next chapter (chap. 3) revealed huge time costs involved when digestively processing crushed shell material. This was experimentally found by measuring consumption rates of captive, fasted knots that were *ad libitum* offered a range of various mollusc prey types. Firstly, all prey types were handled much faster than they were digestively processed. Secondly, digestive processing rate (# prey/s) was inversely related to the amount of shell mass per prey. In other words, the amount of shell mass digestively processed per unit of time was constant across all prey types. In addition, because we had experimentally manipulated gizzard mass (through manipulating the hard-ness of the food on offer *before* the experiment started), we could show that birds with a large gizzard were able to process more shell mass per unit of time than birds with a small gizzard (gizzards were measured using ultrasonography).

The latter observation was an important insight. Using the *quantitative* relationship between rate of digestion and gizzard mass, we were able to calculate what gizzard size was needed for a given daily energy requirement. If a gizzard of a given size can only process a fixed amount of shell mass per unit of time, then we only need to know the amount of flesh per gram shell mass (defined as *prey quality*) to be able to calculate what the maximum daily flesh-consumption will be (the next calculation from flesh to metabolisable energy is an easy one as energetic density and assimilation efficiency are rather constant; note that in all these calculations we assume a fixed daily foraging time). The seasonal variation in daily energy requirements (in the Wadden Sea) was known from earlier work on knots; the seasonal variation in the quality of consumed prey types was calculated from observed diet compositions and published values of flesh-to-shell ratios. This gave us two models about the seasonal variability in gizzard mass of knots living in the Wadden Sea. The first model assumes that knots balance their energy income with their energy expenditure (so-called 'satisficing'); the second model assumes that knots aim to maximise their daily energy income (this constrained maximum is known from the literature). Both models predict enlarged gizzards when ambient temperatures are low and/or when prey qualities are low, where the second model always predicts larger gizzards than the first (in other words, daily energy expenditure rates never come close to the maximum daily energy income). Overlaying the model predictions with real-world data shows that knots using the Wadden Sea maintain satisficing gizzards almost all year round. This is in agreement with their body mass,

which is kept fairly stable throughout the year, except in spring when fuelling for departure to the breeding grounds. It is this time of year during which knots build large, rate-maximising gizzards. In addition, marginal fuelling during midwinter is reflected by the midwinter gizzard masses, which are in between satisficing and rate-maximising size.

Stimulated by the model's success rate, we applied the predictions on optimal gizzard mass to other situations. For example, we calculated the expected gizzard mass of the captive knots from the previous chapter (chap. 2). It turned out that the birds had built gizzards that just balanced their daily energy budgets. The gizzard-model also became the basis for chapter 4. In that paper we predicted gizzard mass at stopovers and at wintering sites for five out of the six recognized subspecies of knot. At each wintering site we found satisficing gizzards, while at each stopover we found rate-maximising gizzards. Again, this was in agreement with the expected energy budget at each site: during winter knots keep their energy budget more or less balanced while at stopovers they try to fuel as fast as possible to be able to reach the breeding grounds in time. However, the unexpected result in this chapter was the observation that rate-maximising gizzards were not larger but smaller than satisficing gizzards! At first glance this seems to be a *contradictio in terminis*, which however can be explained by the much higher prey qualities found at stopovers than at wintering sites. It seems that red knots only pick out *those* stopovers that harbour high-quality food, the so-called 'hotspots' along their migratory flyway. Calculations that take flight costs into account suggest that using those hotspots is a prerequisite to arrive at the breeding grounds in time. Especially tropically wintering knots seem to rely strongly on such hotspot-stopovers (see box X in chapter 11 about the *piersmai*-subspecies). Presumably because of the enormous heat, knots avoid the build-up of rate-maximising gizzards in the tropics. Large gizzards generate a lot of maintenance heat and this could lead to (additional) heat stress in the hot tropics. Therefore, (1) fuelling in the tropics occurs at a slow pace, shrinking the time available to travel. Moreover, (2) tropically wintering knots arrive with small "heat-avoidance gizzards" at the next stopover (there is little time left to drastically increase gizzard mass). Two good reasons why they need super-quality prey along the flyway to arrive in time at the arctic breeding grounds. For the *piersmai*-subspecies we calculated that migration would span 40 days longer if prey at the Chinese stopover were of similar, low quality as those at the tropical, Australian wintering site.

In chapter 5 we return to the Dutch Wadden Sea. There we found prey selections by knots that were in disagreement with the best-known models on optimal diet choice. Those models predict that predators should accept only

those prey types that yield the highest energy gain per unit handling time. Most bivalves fit this description well (short handling times and containing quite some flesh). Of course, red knots are known for their hard-shelled diet, but after calculating their preference (so correcting for the amount on offer), it turned out that knots most liked soft-bodied prey items that carry no shell (small crabs and shrimps). However, handling such manoeuvrable crabs or shrimps takes relatively long and such soft-bodied prey types therefore end up low on the *predicted* preference scale! Again, digestive processing rate turned out be the crux of the story. Earlier we saw that rate of digestion (# prey/s) is inversely related to the amount of indigestible shell mass per prey. If rate of digestion bottlenecks energy intake rate (which is often the case in red knots), then knots better select those prey types that contain as little as possible shell material per gram flesh, i.e. prey of the highest *quality*! Crabs and shrimps are mainly composed of flesh and contain only very little amounts of indigestible matter. Therefore, the long handling time required to swallow these digestible prey does not bother the digestively constrained knot.

In spite of those clear-cut experimental findings, we often find free-ranging knots exploiting patches of hard-shelled prey while ignoring patches of soft-bodied food. This problem is tackled in chapter 6. By intensively tracking radio-tagged knots whose gizzard mass was estimated ultra-sonographically we found that knots carrying a large gizzard mainly visited shellfish patches, while knots carrying a small gizzard mainly visited soft-food patches (differences between individuals in gizzard mass were interpreted as reflecting differences in the timing of arrival from the tundra breeding grounds in the Wadden Sea). Again, insights into digestive processing rates provided the answer. Without being digestively constrained, all knots should only feed in the shellfish patches, simply because shellfish occur in much higher densities than soft-bodied crustaceans, therefore yielding higher encounter rates, subsequently leading to higher intake rates. However, because shellfish-eating knots often face digestive constraints, this could lead to situations where rate of digestive processing at the shellfish patch drops below the intake rate at the soft-food patch, making it energetically more profitable to go for the scarce but high-quality soft-bodied prey. This will happen most in birds with the smallest gizzards, since they have the least capacity to process crushed shell material.

Because energy intake rates can never exceed digestive processing rates, knots with smallest gizzards have the lowest energy intake rates. This was not only apparent in the experiments, but could also be shown indirectly in the field. By daily keeping track when radio-tagged individuals with known gizzard masses left and arrived again at their high-tide roost at Richel we

estimated daily foraging times. This showed that birds with the smallest gizzards fed for about 16-17 hours/day, while birds with the largest gizzards were away from Richel for less than 12 hours/day. We calculated that birds with small gizzards where, in spite of their long working days, only just able to fulfil their daily energy needs, while birds with large gizzards were in positive energy balance.

One of logical questions that came to mind was how knots can be away from Richel for 16 hours a day, while normally mudflats are exposed for only 12 hours a day. The answer lies in the huge tidal differences operating in the western Wadden Sea. Because low tide at Richel occurs two hours before low tide further east at Ballastplaat, a knot can gain two hours extra per tidal cycle, i.e. four hours extra per day. Analyses of the use of space in the western Wadden Sea indeed revealed that red knots extend their low tide period by moving eastwards along with the outgoing tide.

Further analyses of daily feeding itineraries (chap. 7) showed that radio-tagged *islandica*-knots, in spite of the abovementioned 'tide-extension', aim to minimise the distance between their high-tide roost and their feeding grounds. Knots roosting at Griend feed most of their time near Griend, while knots roosting at Richel feed more often near Richel. Very likely, time and energy savings play a major role here. It is however remarkable that the feeding grounds near Griend are generally better than the feeding grounds near Richel and the question arises why some birds prefer Richel above Griend as their roost. It turns out that on average Richel-roosting birds are heavier and have larger gizzards than Griend-roosting birds. Possibly, heavier birds, experiencing impaired manoeuvrability, incur higher predation risks at Griend (in contrast to Richel, Griend has a rather high dike these days, which encourages surprise attacks by raptors and owls). Moreover, heavier birds (and especially those with large gizzards) experience low risks of starvation and they should prefer safety over food. This is also reflected in the amount of time spent feeding during low tide: the heavier the knot (measured by scoring abdominal profiles), the less time devoted to feeding. If heavy knots feed, they do so in the midst of the low tide period, presumably because only then the best feeding sites are exposed. In this way they minimise their daily foraging time (note that we here deal with overwintering *islandica*-knots that aim to *balance* rather than to *maximise* their daily energy budget).

Knots feed close together in large flocks and in chapter 8 we investigate the costs of living socially. Since populations cannot grow unlimited but are regulated by density-dependent processes there must be a cost to living in dense flocks, such as for example the cost of interference competition. Again, digestive processing rate comes into play. The results of an experiment

performed in the 'tidodrome' on Texel suggest that only knots that are *not* digestively constrained pay the price of interference competition. For knots that *are* digestively constrained, a little loss in potential foraging time due to interference interactions does not lead to reduced long-term intake rates. This is because digestively constrained birds can take it easy when searching for prey; they will have to wait anyway before there is some 'digestive space' available. As long as the time lost to competitive interactions overlaps with such digestive pauses there is no direct loss in intake rate (assuming that digestion is not slowed down during interference interactions). Applying this idea, we predicted how close knots can live together when feeding (i.e. aggregative response). We contrasted this prediction to predictions of classical interference models that ignore digestive constraints (and which therefore predict much lower densities of knots). Field-observations on the distance between individual knots agreed with the interference-model taking rate of digestion into account. By contrast, the classical interference models underestimated knot-densities by more than an order of magnitude! Further support for the digestion-based interference model came from the observations that knots feeding on soft-bodied prey tend to feed further apart than shellfish-eating knots. They face less stringent digestive constraints and therefore interference depresses their intake rates at lower competitor densities.

Also depletion, being another form of intraspecific competition, can play a major role in the density-dependent regulation of knot-populations. In order to gain insight in depletion processes and how individual knots cope with depleting food stocks, we performed an experiment with solitary knots feeding in small-scaled food patches (chap. 9). One of the questions that we addressed was how an individual knot estimates the number of prey remaining in a depleting patch. Since its prey live buried in the sediment, a knot is unable to see the prey that are still present. Searching for such hidden prey items is a stochastic process and therefore the time between two prey encounters is not very informative in this respect. It turned out that the experimental birds integrated all the information that their foraging yielded (i.e. the total number of prey found per patch and the total search time per patch). In addition, they appeared to combine this patch sample information with prior knowledge about the expected initial number of prey per patch. Comparing several theoretical models on feeding on hidden prey showed that this particular way of information usage yielded the highest possible prey-encounter rates. What came as an initial surprise was that, in spite of the optimal use of information, the knots left their patches at lower giving-up densities (GUDs) than expected. Again, this could not be understood without using our knowledge on digestion rates. It turned out that the high prey

densities that we offered lead to digestive constraints in the experimental birds. Therefore, 'hurrying up' and leaving patches at high GUDs was of no use. It would only lead to higher prey *encounter* rates but, because of digestive constraints, it would never lead to higher prey *ingestion* rates. The knots would better slowdown by staying longer at a patch. In this way they reduced travel-costs and maximised their (long-term) net energy intake.

Depletion rates also form the basis for chapter 10, where we extend existing models on carrying capacity by using fitness-based models on patch use. Carrying capacity is here defined as the time that a given number of animals can be sustained by a given, non-renewable food source. Existing carrying capacity models assume that animals give up their food source when gross energy intake rate no longer covers energy expenditure (which occurs at a fixed, so-called *critical* prey density). However, current models on patch use assume that animals also take risk of predation and the quality of alternative sites into account when deciding to abandon a food source (which then occurs at variable, so-called *giving-up* density). By combining both approaches we show that the classical carrying capacity models may either over- or underestimate carrying capacity. We conclude this chapter by pinpointing at the terminological confusion in the recent literature on the difference between *critical* and *giving-up* densities.

We end this thesis by stressing two critical phases in the annual cycle of the knot: spring- and autumn-migration (chap. 11). During the northbound spring-migration, knots are forced to select only those stopovers that harbour high-quality prey (so-called 'hotspots'). Only then will fuelling with relatively small gizzards be fast enough, such that the breeding grounds will be reached in time (the usage of hotspots seem especially crucial for the tropically wintering subspecies). Because of this strong link with the timing of arrival in the arctic, this phase is especially critical for an individual's *reproductive success.*

Crucial for *survival* seems the southward fall migration and the subsequent settlement on the wintering sites. It seems that *canutus*-knots skip the Wadden Sea as their stopover and continue travelling to West-Africa in years when soft-bodied crustaceans are scare (which presumably impairs their survival chances during the subsequent prolonged flight). An additional complication is the strong exploitative competition for soft-bodied prey: calculations backed-up by data show that the preferred soft food can be fully depleted within a month's time. A knot better hurries up leaving its breeding grounds.

Islandica-individuals seem to take prey quality into account when deciding whether to overwinter in the Wadden Sea or not. In years with relatively poor-quality prey we only caught birds with large gizzards; by contrast, in years with relatively high-quality prey we caught birds with small gizzards. At

first glance, we interpreted this as adequate gizzard size adjustments of individual birds to food quality. However, after thorough analyses of colouring-resighting rates, we found a strong correlation between local survival rate in the Wadden Sea and local prey quality. In other words, more birds seem abandon the Wadden Sea in years with poor-quality prey than in years with high-quality prey. It turned out that birds that left the Wadden Sea were birds with the smallest gizzards, which was the main reason for the annual fluctuations in average gizzard mass. We calculated that the amount of fat present in just-arrived *islandica* only allows a 1-gram increase in gizzard mass. By combining this insight with the observed distribution of gizzard masses upon arrival, we correctly predicted annual local survival as a function of local prey quality.

It appears that the inter-annual variability in prey quality is not just random noise. Rather it seems that mechanical cockle-fisheries have played a major role here. This became evident after detailed analyses of the exact fishing locations (automatically registered by so-called 'black boxes' onboard of the ships). Quality of small, ingestible cockles had declined most (35%) at sites that were fished most often (three out of four years), while cockle quality was constant at sites that were never fished. Possibly, this is caused by an increase in the local sediment-coarseness or changes in other, unidentified sediment characteristics, which has been shown to occur at sites that have been mechanically dredged. Other work on another bivalve species (the Baltic tellin; dissertation Drent) shows that the foraging apparatus and possibly food intake is largely governed by sediment grain size. In short, it seems valid to conclude that, through sediment-related effects on prey quality, mechanical shellfisheries have reduced local survival of *islandica*-knots in the Wadden Sea.

Time will tell whether these effects on *local* survival can be found back in *true* survival. Knots are mobile and relatively long-lived, and therefore individuals that were declared dead, might reappear in the Wadden Sea in better times. However, the paucity of observations elsewhere, e.g. on the British Isles, suggests that the dispersal to alternative overwintering sites indeed leads to additional mortality. To really find out, it is therefore of utmost importance to continue these population-dynamical measurements (dispersion, survival, and recruitment) for many more years, hand in hand with measurements on the quality of the environment (notably the food). This not only serves the science of ecology, but can also contribute to the conservation of this vulnerable species.